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Running head: Disturbance and competitive coexistence

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Abstract. Disturbance plays a key role in structuring community dynamics and is central to conservation and natural resource management. However, ecologists continue to debate the importance of disturbance for species coexistence and biodiversity. Such disagreements may arise in part because few studies have examined variation across multiple dimensions of disturbance (e.g., size, frequency) and how the effects of disturbance may depend on species attributes (e.g., competitiveness, dispersal ability). In light of this gap in understanding and accelerating changes to disturbance regimes worldwide, we used spatial population models to explore how disturbance size and frequency interact with species attributes to affect coexistence between seagrass (*Zostera marina*) and colonial burrowing shrimp (*Neotrypaea californiensis*) that compete for benthic space in estuaries throughout the west coast of North America. By simulating population dynamics under a range of ecologically-relevant disturbance regimes, we discovered that intermediate disturbance (approximately 9–23% of landscape area per year) to short-dispersing, competitively-dominant seagrass can foster long-term stable coexistence with broad-dispersing, competitively-inferior burrowing shrimp via the spatial storage effect. When holding the total extent of disturbance constant, the individual size and annual frequency of disturbance altered landscape spatial patterns and mediated the dominance and evenness of competitors. Many small disturbances favored short-dispersing seagrass by hastening recolonization, whereas fewer large disturbances benefitted rapidly-colonizing burrowing shrimp by creating temporary refugia from competition. As a result, large, infrequent disturbances generally improved the strength and stability of coexistence relative to small, frequent disturbances. Regardless of disturbance size or frequency, the dispersal ability of the superior competitor (seagrass), the competitive ability the inferior competitor (burrowing shrimp), and the reproduction and survival of both species strongly influenced population abundances and coexistence. Our results show that disturbance size and frequency can promote or constrain coexistence by altering the duration of time over which inferior competitors can escape competitive exclusion, particularly when colonization depends on the spatial pattern of disturbance due to dispersal traits. For coastal managers and conservation practitioners, our findings indicate that reducing particularly large disturbances may help conserve globally-imperiled seagrass meadows and control burrowing shrimp colonies that can threaten the viability of oyster aquaculture.

Keywords: *biodiversity; burrowing shrimp; dispersal; estuary; intermediate disturbance hypothesis; population dynamics; seagrass; sensitivity analysis; spatial ecology; storage effect*

Introduction

Understanding how spatial processes promote or constrain species coexistence is an enduring challenge in ecology. According to theory, coexistence of competitors at landscape scales requires that differences among species in competitive abilities are offset by niche or life-history differences, such as their dispersal ability, resource use, or response to disturbance or natural enemies (Holt 1985, Chesson 2000, Amarasekare 2003, Kneitel and Chase 2004, Roxburgh et al. 2004). For example, when species exhibit competition–colonization trade-offs, inferior competitors rapidly colonize available patches and disperse offspring prior to being displaced by slow-colonizing superior competitors (Levins and Culver 1971, Tilman 1994). For long-term stable coexistence, dominant competitors cannot occupy all space but instead must suffer loss from disturbances, senescence, or natural enemies that cause spatiotemporal heterogeneity in the stages of succession (Amarasekare 2003, Roxburgh et al. 2004).

Disturbances (i.e., discrete events that change resources or the physical environment and disrupt ecosystem structure; White and Pickett 1985) have been focal to the study of coexistence because they often simultaneously mediate competitor abundance and resource availability. For example, disturbance to dominant plants can alter competitive dominance and resources to reorganize communities in forests (Ellison et al. 2005), grasslands (Collins 2000), and coastal marine ecosystems (Williams 1990, Castorani et al. 2014, 2018). Despite strong evidence that disturbance often mediates community structure, there has been mixed support for the longstanding hypothesis that intermediate levels of disturbance foster coexistence and enhance biodiversity (Connell 1978, Huston 1979, 2014, Mackey and Currie 2001, Hughes et al. 2007, Mayor et al. 2012, Fox 2013, Sheil and Burslem 2013). However, investigations of the intermediate disturbance hypothesis typically focus on individual elements of disturbance (e.g., size, frequency; Miller et al. 2011, 2012, Zhang and Shea 2012, Castorani et al. 2018) or treat them as interchangeable (Connell 1978, Miller 1982, Amarasekare 2003). Hence, disagreements and uncertainty in disturbance-diversity relationships may be partly

resolved if different disturbance elements vary in their effects on coexistence or if effects depend upon relevant species attributes (e.g., competitiveness, dispersal ability).

Resolving how variation in different elements of disturbance mediates coexistence is a pressing challenge because humans alter disturbance regimes in many ecosystems (Turner et al. 2003, Ellison et al. 2005). Moreover, the severity (size or magnitude of impact) and frequency (number of events within a time period) of many disturbances have increased or are forecast to increase due to climate change (Ummenhofer and Meehl 2017). Clarifying the ways that different disturbance elements influence the persistence of competitors is also valuable to biodiversity conservation and natural resource management. For example, depressing disturbance frequency (e.g., fire suppression) can improve the recovery of target species (Coffin and Lauenroth 1988) or threaten the persistence of conserved taxa with low competitive rank (Collins 2000). Similarly, increasing disturbance frequency can diminish richness (Turner et al. 2003), enhance richness (Cavender-Bares and Reich 2012), or both depending on species attributes (Castorani et al. 2018). Manipulating disturbance regimes can also aid in the control of undesired species, such as agricultural pests and non-native species (Zhang and Shea 2012).

In light of these basic and applied challenges, we explored how variation in disturbance size (individual diameter), frequency (number per year), and their interaction alter long-term landscape-scale coexistence. We focused on competition for space because it is a limiting resource in numerous ecosystems (or a proxy for other spatially-constrained resources such as light, water, or food) and is commonly mediated by disturbance to space-holding organisms. Specifically, we explored how disturbance structures coexistence between seagrass and colonial burrowing shrimp that compete for dominance of benthic habitats in estuaries and shallow seas worldwide (Suchanek 1983, Harrison 1987, Dumbauld and Wyllie-Echeverria 2003, Siebert and Branch 2006, Berkenbusch et al. 2007). Seagrass and burrowing shrimp are ideal study species because they exhibit a classic competition–colonization trade-off (Castorani et al. 2014) and benthic disturbance is commonly managed to promote seagrass conservation (Waycott et al. 2009) or burrowing shrimp eradication (Dumbauld et al. 2006). By using this well-described empirical system to investigate how ecologically-relevant variation in disturbance size and frequency structures coexistence, our approach aims to bridge the divide between findings from models and data (e.g., Mackey and Currie 2001, Hughes et al. 2007,

Mayor et al. 2012, Fox 2013, Huston 2014) and brings advantages of realism over prior theoretical studies that used generic competition models (e.g., Banitz et al. 2008, Miller et al. 2012, Liao et al. 2016; but see Moloney and Levin 1996).

Within the context of our study system, we asked the following questions: (1) How does the total extent of disturbance influence the coexistence of spatial competitors and does biodiversity peak at intermediate levels of disturbance? (2) Do changes in disturbance size and frequency mediate the effects of disturbance extent in structuring the coexistence and relative abundance of competitors? (3) What mechanisms promote stable coexistence? (4) How important is intraspecific variation in biological attributes (e.g., demographic parameters) and is this importance mediated by variation in disturbance size or frequency?

To address these questions, we varied disturbance using spatially-explicit population models because conducting sufficiently large, numerous, or frequent disturbances in the field can be impractical and unethical, while natural experiments commonly conflate multiple disturbance attributes (Castorani et al. 2018). We varied disturbance size and frequency to determine their combined effects on long-term coexistence and used sensitivity analysis to assess how biological attributes affect species abundances. Our results broaden theory on biodiversity in heterogeneous landscapes by comprehensively investigating how the size and frequency of disturbance interact with variation in competitiveness, dispersal ability, and demographic processes to structure species coexistence.

Methods

Study system. Throughout the west coast of North America, the bottoms of shallow estuaries and coastal lagoons are commonly dominated by undersea meadows of seagrass (eelgrass *Zostera marina*), dense colonies of burrowing shrimp (ghost shrimp *Neotrypaea californiensis*), or a co-dominant patch mosaic of both species (Fig. 1A; Appendix S1; Harrison 1987, Swinbanks and Luternauer 1987, Castorani et al. 2014). These two benthic species exhibit a competition–colonization trade-off. Ghost shrimp are locally excluded by the physical structure of eelgrass rhizomes and roots (which inhibit surface burrows; Brenchley 1982, Castorani et al. 2014) but rapidly colonize areas where eelgrass is lost to disturbances (Harrison 1987, Castorani et al. 2014) such as storms that cause

wave scour or sand burial, marine heatwaves, algal blooms, overgrazing, and coastal development, which are common in shallow estuaries (Short and Wyllie-Echeverria 1996). Although competitively dominant, eelgrass can be relatively slow to recover from such disturbances due to limited distances of rhizome elongation (≤ 2–3 m/y; Marbà and Duarte 1998) and seed dispersal (typically ≤ 5–10 m; Orth et al. 1994, Ruckelshaus 1996, Furman et al. 2015; but see Källström et al. 2008), particularly when compared to the much broader scales of ghost shrimp larval recruitment (Kozuka 2008) and adult lateral movement (about 1–13 m/y; Posey 1986b, Weitkamp et al. 1992, Castorani et al. 2014). Hence, field experiments support the hypothesis that the extent and pattern of eelgrass disturbance mediate competitive exclusion of burrowing shrimp (Harrison 1987, Castorani et al. 2014).

Eelgrass and other seagrasses are focal to coastal conservation due to their global declines from anthropogenic activities in spite of high value as habitat-forming foundation species (Waycott et al. 2009). Although native, ghost shrimp are the target of eradication in some regions of commercial oyster aquaculture because their bioturbation kills young bottom-cultured oysters (Feldman et al. 2000). Since adult ghost shrimp can migrate up to a meter below the sediment surface, they are highly resistant to disturbances that cause eelgrass loss, as evidenced by decades of unsuccessful attempts to control burrowing shrimp colonies by mechanical disturbance or compaction of sediments (Washington State Department of Ecology 2015).

Population dynamics. To explore how the total extent, size, and frequency of disturbance interact with biological attributes to structure the coexistence and abundance of competing seagrass and burrowing shrimp, we developed spatially-explicit population models (Fig. 2) using data on both species' demography, growth, reproduction, competition for space, and mortality (due to disturbance and non-disturbance factors). Specifically, we used a set of discrete-time difference equations to model the annual population dynamics of seagrass shoots ($S_{ij,t}$) and seeds ($E_{ij,t}$), and burrowing shrimp adults ($B_{ij,t}$) and juveniles ($Y_{ij,t}$) in each year (t) and patch (patch i, j centered at location x_i, y_j in a two-dimensional landscape). We used a stage-structured model for both species to account for differences in dispersal ability, interactions, and susceptibility to disturbance of each stage. We parameterized our model using data or estimates from the literature and simulated population dynamics across a range of disturbance regimes that differed in the individual size and annual frequency of ecologically-relevant disturbances to seagrass. In particular, we simulated disturbances that cause the complete mortality of

seagrass shoots (all aboveground and belowground tissues), such as severe storms. Lastly, to assess how intraspecific variation in the biological attributes of both species affects competitor abundances, we performed a global sensitivity analysis under multiple disturbance regimes (Harper et al. 2011).

Seagrass populations grow through both sexual and asexual reproduction. A proportion of seagrass shoots develop into senescent flowering shoots and produce seeds, together leading to per capita reproduction σ (Olesen 1999). We assumed seagrass per capita reproduction was constant over space because, in general, flowering effort does not differ based on seagrass patch size or shape (Livernois et al. 2017, Stubler et al. 2017), seed production does not vary based on patch size or within-patch location (Harwell and Rhode 2007; Stubler et al. 2017), and germination is not density-dependent (Orth et al. 2003). Seeds dispersed radially from all source patches (i', j') following a Gaussian probability density function (PDF) with standard deviation ω. Because eelgrass seeds are not viable after about 12 months (Moore et al. 1993, Jarvis et al. 2014), non-germinating seeds suffered total mortality after one year. Hence, seed abundance each year depended entirely on production from flowering seagrass shoots in the same year according to:

$$E_{ij,t} = \sum_{i'=1}^{n_i} \sum_{j'=1}^{n_j} \left[\sigma S_{i'j',t} \cdot \frac{1}{\pi\omega^2} e^{-\left(\sqrt{(x_i - x_{i'})^2 + (y_j - y_{j'})^2}/\omega\right)^2} \right]. \quad \text{(Eq. 1)}$$

A fraction (γ) of seeds germinated and survived to adulthood (i.e., became seagrass shoots). To account for additional mortality of young seed recruits through sediment reworking by ghost shrimp (Dumbauld and Wyllie-Echeverria 2003), we integrated the instantaneous rate of bioturbation-driven mortality (ψ) per adult burrowing shrimp over one year. Seagrass shoots propagated new shoots asexually in proportion (α_S) to the local (i.e., within-patch) abundance of adult shoots (Marbà and Duarte 1998). Of these new clonal shoots, a proportion ($1 - l$) remained within their natal patch and the remainder (l) spread laterally and uniformly contributed to populations in N neighboring patches, defined as those separated by distances less than the annual rate of rhizome elongation (d). Existing seagrass shoots experienced constant, density-independent mortality due to non-disturbance factors, such as senescence or herbivory (Olesen and Sand-Jensen 1994a), with proportion μ_S surviving. Combining surviving shoots with those produced from sexual and asexual reproduction yielded the new seagrass shoot population:

$$F_S(S_{ij,t},\, E_{ij,t},\, B_{ij,t}) \;=\; \alpha_S(1-l)S_{ij,t} \;+\; \frac{\sum_{i'=1}^{n_i}\sum_{j'=1}^{n_j}}{\sqrt{(x_i-x_{i'})^2+(y_j-y_{j'})^2}<d}\left(\alpha_S\left[\frac{l}{\hat{N}}\right]S_{i'j',t}\right) + \gamma e^{-(\psi B_{ij,t})}E_{ij,t} + \mu_S S_{ij,t}\,. \qquad \text{(Eq. 2)}$$

New and surviving seagrass shoots underwent Beverton-Holt density-dependent competition for space, saturating at $1/\beta_S$ (Table 1). Shoots suffered complete mortality within disturbed patches (i.e., $D_{ij,t} = 0$ for disturbance in patch ij and year t; otherwise $D_{ij,t} = 1$). Thus, the abundance of seagrass shoots after density dependence and disturbance was:

$$S_{ij,t+1} \;=\; \frac{F_S(S_{ij,t},\, E_{ij,t},\, B_{ij,t})}{1 \;+\; \beta_S F_S(S_{ij,t},\, E_{ij,t},\, B_{ij,t})} \;\times\; D_{ij,t}\,. \qquad \text{(Eq. 3)}$$

Young burrowing ghost shrimp mature through a series of pelagic larval stages. After being released by adult females during spring and summer, larvae develop in nearshore waters for 4–6 weeks (Johnson and Gonor 1982, Dumbauld et al. 1996, Morgan et al. 2011). Larvae then return to estuaries and settle to the bottom as juveniles. Because ghost shrimp larval recruitment depends upon the adult population size but is highly variable over time (Dumbauld et al. 1996, Feldman et al. 1997, 2000, Dumbauld and Bosley 2018), we assumed that the annual abundance of juveniles was determined by a time-varying stochastic process in proportion ($\alpha_{B,t}$) to the total abundance of adults (i.e., the population was demographically closed). We further assumed that recruitment was uniform across the landscape (Dumbauld and Bosley 2018). Juveniles matured (i.e., left the juvenile class) at rate ρ. Both juvenile and adult burrowing shrimp experienced constant, density-independent mortality (μ_B) from processes including predation and senescence (Posey 1986b, Weitkamp et al. 1992, Dumbauld et al. 2008, Castorani et al. 2014). Combining new recruits with surviving juveniles that do not mature yielded the juvenile population of burrowing shrimp:

$$Y_{ij,t+1} \;=\; \alpha_{B,t}\sum_{i'=1}^{n_i}\sum_{j'=1}^{n_j}\left(\frac{B_{i'j',\,t}}{n}\right) \;+\; \mu_B e^{-\rho} Y_{ij,t}\,. \qquad \text{(Eq. 4)}$$

Adult ghost shrimp can rapidly colonize adjacent habitats by burrowing laterally (Harrison 1987, Castorani et al. 2014, Dumbauld and Bosley 2018) and thus we approximated the radial movement of adult burrowing shrimp populations as a Gaussian PDF dependent on the annual lateral movement rate (ζ). Seagrass competition caused local declines in adult burrowing shrimp abundance at rate φ per seagrass shoot (Castorani et al. 2014). Combining newly maturing juveniles with surviving burrowing shrimp adults yielded:

$$F_B(S_{ij,t},\, B_{ij,t},\, Y_{ij,t}) \;=\; \left([1 - e^{-\rho}] Y_{ij,t} \;+\; \sum_{i'=1}^{n_i} \sum_{j'=1}^{n_j} \left[\frac{1}{\pi \zeta^2} e^{-\left(d_{ij,i'j'} / \zeta \right)^2} \right] B_{i'j',t} \right) \mu_B e^{-\varphi S_{ij,t}} . \quad \text{(Eq. 5)}$$

Newly recruited and surviving burrowing shrimp underwent Beverton-Holt density-dependent competition for space (Dumbauld et al. 1996), saturating at $1/\beta_B$ (Table 1), leading to the new adult burrowing shrimp abundance:

$$B_{ij,t+1} \;=\; \frac{F_B(S_{ij,t},\, B_{ij,t},\, Y_{ij,t})}{1 \;+\; \beta_B F_B(S_{ij,t},\, B_{ij,t},\, Y_{ij,t})} . \quad \text{(Eq. 6)}$$

Disturbance. We varied the individual size (all integers from 1 to 40 m diameter, inclusive) and annual frequency (all integers from 1 to 1604 per year, inclusive) of disturbance to seagrass using all possible combinations that resulted in approximately 0–50% of the total landscape area disturbed per year (2,577 unique combinations), representing disturbance regimes characteristic of our study system (Short and Wyllie-Echeverria 1996). For each year and simulation, we varied the location of disturbance centroids across the landscape by randomly sampling (without replacement) from a uniform distribution of all possible patches. Disturbances falling outside of landscape boundaries or overlapping with other disturbances were not redistributed elsewhere within the landscape. Therefore, to avoid any biases from areas of disturbance 'lost' outside of landscape boundaries or overlapping with other disturbances, in all analyses we investigated the effect of the actual proportion of the total landscape area disturbed per year and averaged these across all years within each simulation (i.e., the output values of realized disturbance, not the input values of the simulated disturbance regime).

Simulations. We simulated the model landscape in R 3.4.4 (R Core Team 2018) with a two-dimensional lattice of regular hexagonal patches (n = 3,600 patches, simulating 60 m × 60 m; Fig. 1B) characteristic of the scale of interspecific interactions (diameter = 1 m; area = 0.866 m^2; Castorani et al. 2014). We discretized space using a hexagonal tessellation because it has ideal patch-neighbor symmetry and approximates radial dispersal more accurately than Cartesian grids (Birch et al. 2007). We indexed patches using integer hexagonal coordinates (i, j) and measured inter-patch distances using the location of patch centroids in Cartesian space (x_i, y_j).

Dispersal beyond landscape boundaries resulted in mortality because eelgrass dies from light stress at depth (Dennison 1987), and temperature or desiccation stress in the intertidal (Marsh et al. 1986, Boese et al. 2005). Likewise, predation can restrict ghost shrimp from colonizing deep zones

(Posey 1986b, Weitkamp et al. 1992), and bait fishing or pesticide application can limit intertidal distributions (Peterson 1977, Dumbauld et al. 1996).

For each disturbance regime we performed 20 numerical simulations of annual population dynamics for 250 years, which was sufficient for populations to reach quasi-equilibria given environmental and demographic stochasticity. Additional replicate simulations (up to 200) and longer durations (up to 10,000 years) did not change mean abundances or coexistence predictions (Appendix S2: Figs. S1–S2). We initiated all simulations by randomly selecting each patch to start with either a small number of seagrass shoots or a small number of adult burrowing shrimp (other starting conditions changed the time needed to reach quasi-equilibria, but did not change coexistence or abundances at quasi-equilibria). During each simulation we tracked the annual landscape-scale densities of seagrass shoots ($S_t = \sum_{i'=1}^{n_i}\sum_{j'=1}^{n_j}\left[\frac{S_{i'j',t}}{n}\right]$) and adult burrowing shrimp ($B_t = \sum_{i'=1}^{n_i}\sum_{j'=1}^{n_j}\left[\frac{B_{i'j',t}}{n}\right]$). For both species, we normalized abundances by dividing annual densities by the maximum observed density across all simulations ($\overline{S}_t = \frac{S_t}{S_{max}}$; $\overline{B}_t = \frac{B_t}{B_{max}}$). As an index of the strength of coexistence and relative parity in normalized abundances we also measured species evenness using Simpson's E (Simpson 1949), which ranged from 0.5 to 1. Lastly, to characterize landscape-scale population patterns we measured the spatial autocorrelation of normalized seagrass and burrowing shrimp abundances using Moran's I (Moran 1950). For each disturbance regime, we calculated metric averages across simulations at quasi-equilibria.

Parameterization and sensitivity analysis. To parameterize the biological components of our model, we obtained values from the peer-reviewed literature and used the mean of these estimates for our simulations (Table 1). We estimated the seagrass seed dispersal parameter (ω) by fitting a Gaussian kernel to *in situ* eelgrass seed dispersal data (Appendix S3: Fig. S1). We approximated stochastic variation in burrowing shrimp recruitment among years by randomly choosing the annual recruitment density parameter ($\alpha_{B,t}$) from a truncated normal distribution of possible values (Table 1). We estimated the effect of seagrass competition on burrowing shrimp (φ) by fitting a negative exponential relationship to *in situ* density data (Appendix S4: Fig. S1). For seagrass populations, we parameterized β_S (which sets the saturation point of Beverton-Holt density dependence) as $\beta_S = \frac{\mu_S + \alpha_S - 1}{(\mu_S + \alpha_S)k_S}$ so that the equilibrium seagrass population density in the absence of shrimp was near the

observed carrying capacity (k_S). Likewise, for burrowing shrimp populations we parameterized β_B as $\beta_B = \frac{\mu_B + \alpha_B - 1}{(\mu_B + \alpha_B)k_B}$. We estimated the shrimp maturation rate ρ as the inverse of the average time to maturity (2–4 years; Pimentel 1986, Dumbauld et al. 1996).

To quantify the relative influence of variation in species attributes on competitor abundances, we performed a global sensitivity analysis (GSA) by randomly drawing all biological parameter values from uniform distributions across their estimated ranges (Table 1). For each of the resulting 2,000 randomly drawn combinations, we measured landscape-scale abundances of seagrass shoots and adult burrowing shrimp, and species evenness at quasi-equilibria. We analyzed these results with a GSA method that incorporates non-additive and interactive effects using random forest nonparametric bootstrapping (Harper et al. 2011). Using several R packages (*randomForest* 4.6-12, Liaw and Wiener 2002; *rpart* 4.1-12, Therneau and Atkinson 2018; *rpart.plot* 2.1.1, Milborrow 2017), we produced multiple pruned classification and regression trees and used these to rank parameters according to their total effect on species abundances (Harper et al. 2011). We calculated the relative importance of each parameter by comparing the prediction accuracy of trees with and without the parameter and rescaled all importance values so that they summed to one. To assess how disturbance size and frequency affected the importance of biological parameters, we used this GSA approach under four disturbance regimes that supported strong coexistence and parity (Simpson's $E \geq 0.9$) with mean-estimated parameter values: many small disturbances (783 1-m disturbances per year); several medium disturbances (102 3-m disturbances per year); a few large disturbances (13 7-m disturbances per year); and a single very large disturbance (one 21-m disturbance per year).

Stability of coexistence. We evaluated whether coexistence was stable by calculating the realized (stochastic) per-capita growth rates for each species when rare (i.e., Lyapunov exponents). Coexistence occurs when each species can increase when rare and in the presence of its competitor (Chesson 2000). To calculate realized growth rates, for each species we ran stochastic simulations in which the abundance of the focal species was set to zero and the competing species was present at normal abundance. From these simulations we determined the density-independent growth factor (i.e., the projected total population size, for all demographic stages in all patches and without intraspecific competition, at the subsequent time point divided by the total population size at the previous time point, if it was non-zero) through time as $\lambda_{X,t}$ for species X. Hence, we calculated the average realized

growth factor as $\overline{\lambda_X} \approx \frac{1}{T_f}\sum_1^{T_f} ln(\lambda_{X,t})$, given T_f time points (150 years) following a burn-in period (100 years), for all 68 disturbance regimes (n = 20 simulations each) that appeared to support moderate to strong coexistence in the multi-species simulations (E > 0.6). Stable coexistence occurs when $\overline{\lambda_X} > 0$ for both species (Roth and Schreiber 2014, Benaïm and Schreiber 2019).

Coexistence mechanisms. To understand how disturbance structures biodiversity, it is important to clarify the general mechanisms promoting coexistence (Amarasekare 2003). We hypothesized that the 'spatial storage effect' could be an important mechanism underlying disturbance-mediated regional coexistence of seagrass and burrowing shrimp. Under this theory, spatially-varying environmental conditions (e.g., disturbance) favor different species in different patches, and high population growth in favorable patches buffer against low population growth in unfavorable patches (Chesson 2000, Sears and Chesson 2007). Hence, we evaluated whether disturbance promoted coexistence through the spatial storage effect by assessing three requirements: (1) differential responses to the environment, (2) buffered population growth, and (3) covariance between the environment and competition (Chesson 2000).

The first criterion was satisfied because species-specific differences in response to the environment were a fundamental part of the model, as seagrass was killed by disturbance but burrowing shrimp were unaffected. The second criterion was also satisfied because buffered population growth is inherent to spatial population models (Chesson 2000). To evaluate the third criterion, we tested for covariance between the response to the environment and the strength of interspecific competition by simulating population dynamics for each species in the presence and absence of its competitor (using the parameterization described previously) for all 68 disturbance regimes that appeared to support moderate to strong coexistence in the multi-species simulations (E > 0.6). Then, for the individual and combined demographic stages of each species at t = 250, we characterized the environmental response as the natural log of local (patch-scale) abundance in the absence of interspecific competition (i.e., single-species simulations) and characterized the competitive response as the log response ratio of local abundance in single-species (absence of competition) and multi-species (presence of competition) simulations (Sears and Chesson 2007, Berkley et al. 2010). We averaged environmental and competitive responses within each disturbance

regime and estimated the strength of covariance using linear regressions (Sears and Chesson 2007, Berkley et al. 2010).

Results

Effects of the total extent, size, and frequency of disturbance. Increases in the total annual extent of disturbance (i.e., the combined landscape area disturbed each year) caused gradual reductions in seagrass abundance and, beyond a threshold, increases in burrowing shrimp abundance (Figs. 3, 4). Disturbance exceeding about 23% of the total landscape extent per year caused effective extinction of seagrass (i.e., < 1% of the of the observed maximum abundance; Figs. 3A, 4B). Disturbance below about 9% of the total landscape extent per year resulted in the effective extinction of ghost shrimp as a result of being locally outcompeted by seagrass (Figs. 3B, 4C). Ghost shrimp persisted when the total normalized seagrass abundance across the landscape was less than about 0.1 (i.e., 10% of the observed maximum abundance of seagrass; Fig. 5). Hence, coexistence was strongest when about 10–20% of the landscape extent was disturbed per year (cf. green areas in Figs. 4A with warm-colored areas in Fig. 4D). Such disturbance regimes supported coexistence that was generally stable (see *Stability of coexistence*, below) and remained consistent for at least 10,000 years (Appendix S2: Fig. S2).

Disturbance size and frequency mediated how the total annual extent of disturbance affected the abundance and coexistence of seagrass and burrowing shrimp. When holding the total annual extent of disturbance constant, disturbance regimes characterized by fewer large disturbances resulted in less seagrass (Figs. 3A, 4B, 5) and more burrowing shrimp (Figs. 3B, 4C, 5) than regimes with many small disturbances. As a result, larger disturbances generally improved parity in competitor abundance (i.e., increased evenness; Figs. 4D, 5), increased the stability of coexistence (see *Stability of coexistence*, below), and broadened the range in the total extent of disturbance that led to coexistence (cf. Figs. 3A and 3B). A single species (seagrass or burrowing shrimp) dominated the landscape for all but a narrow combination of disturbance sizes and frequencies (i.e., areas in Fig. 4D where species evenness exceeds about 0.5).

Disturbance size mediated seagrass abundance when the total extent of disturbance was below about 23% per year (Fig. 3A), but this effect was most pronounced under moderate disturbance

regimes (about 5–14% of area per year; Fig. 3A). For example, despite the total extent of disturbance being equivalent at about 10% per year, landscapes impacted by a single 22-m disturbance per year resulted in 82% less seagrass than landscapes impacted by nearly 350 1-m disturbances per year (normalized abundance of seagrass = 0.08 and 0.41, respectively; cf. Figs. 4A and 4B). Within the zone of coexistence (about 9–23% of landscape extent disturbed per year; Fig. 3), increases in the individual size of disturbance were matched by strong increases in burrowing shrimp abundance despite no changes in overall seagrass abundance (Fig. 5).

The spatial autocorrelation of seagrass and burrowing shrimp increased with both the individual size and annual frequency of disturbance (Fig. 6). When disturbances were small and frequent, both species were nearly randomly dispersed across the landscape (Moran's $I \approx 0$). Larger infrequent disturbances caused greater clustering (Moran's $I > 0$) for both species, although burrowing shrimp were always more clustered than seagrass (cf. Figs. 6A and 6B). Clustering was also more variable for seagrass, particularly for large, infrequent disturbances (Fig. 6A). For all disturbance regimes, both species were never perfectly dispersed but instead either randomly dispersed or clustered across the landscape (i.e., Moran's I was always positive).

Relative importance of biological parameters. For the four tested disturbance regimes that supported strong coexistence, random forest GSA explained 75% of the variance in relative seagrass abundance and 50% of the variance in relative burrowing shrimp abundance. Parameters describing seagrass reproduction (asexual shoot production, seed production, and seed recruitment), equilibrium shoot density, and shoot survival were most important to seagrass populations, whereas other seagrass parameters and all burrowing shrimp parameters were of little importance to seagrass populations (compare parameters in Fig. 7A). The rate of seagrass lateral spread was among the most important parameters for burrowing shrimp populations, along with those describing burrowing shrimp survival, reproduction, and equilibrium density (Fig. 7B). Interestingly, the ability of burrowing shrimp to inhibit seagrass seed germination via bioturbation was fairly important for burrowing shrimp populations (Fig 7B).

In contrast to large differences among parameters in their importance to seagrass and burrowing shrimp populations, variation in the size and frequency of disturbance had modest effects on parameter importance values, causing small changes in their relative importance but not changing

their order of importance (compare bars of different shades in Fig. 7). Large, infrequent disturbances slightly enhanced the importance of parameters promoting overall seagrass abundance (equilibrium density, shoot survival, asexual reproduction) relative to those promoting rapid seagrass recovery (shoot spread, seed production, seed recruitment). These shifts may have arisen because larger disturbances *per se* depressed overall seagrass abundance, thereby enhancing the importance of factors controlling the size of the seagrass population remaining after disturbance. In contrast, the relative effects of these parameters were more similar when disturbances were small and frequent. For burrowing shrimp, larger disturbances slightly diminished the importance of shrimp equilibrium density and slightly enhanced the importance of seagrass seed mortality by shrimp burial, possibly because larger disturbances enhanced burrowing shrimp persistence within disturbed patches. For all other parameters, variation in disturbance size and frequency had weak or inconsistent effects.

Stability of coexistence. Coexistence was stable for the large majority of disturbance regimes that yielded moderate to high species evenness ($E > 0.6$). Average realized low-density per capita growth rates were always positive for seagrass and positive for burrowing shrimp in 88% of simulations (Appendix S5: Fig. S1). Large, infrequent disturbance regimes generally enhanced growth factors for both species relative to small, frequent disturbances, where burrowing shrimp occasionally had slightly negative growth factors (Appendix S5: Fig. S2). Still, on average, coexistence was stable for all disturbance regimes with moderate to high species evenness.

Coexistence mechanisms. Consistent with theory, patterns of covariance between the environment and competition indicated that coexistence was promoted through the spatial storage effect. Individual and combined abundances of adult and juvenile burrowing shrimp exhibited positive covariance between their responses to the environment and competition ($R^2 = 25.3\%$ for adults, $R^2 = 63.5\%$ for juveniles, and $R^2 = 39.7\%$ for adults and juveniles combined; Appendix S6: Fig. S1), indicating that interspecific competition limits the growth of burrowing shrimp populations in suitable patches (Chesson 2000, Sears and Chesson 2007). Consistent with the inferior competitive strength of burrowing shrimp, individual and combined abundances of seagrass shoots and seeds exhibited weak environment-competition covariance ($R^2 \leq 8\%$; Appendix S6: Fig. S1).

Discussion

Disturbances vary in their size and frequency across a broad range of ecosystems (Turner et al. 2003, Ellison et al. 2005). Despite accelerating changes to disturbance regimes globally (Ummenhofer and Meehl 2017), resolving how such disturbance elements interact with species attributes to structure coexistence and biodiversity has remained a persistent challenge in community ecology (Miller 1982, Chesson 2000, Amarasekare 2003, Miller et al. 2012, Huston 2014, Castorani et al. 2018). Our findings help narrow this gap by supporting three general conclusions about how disturbance can structure the coexistence of species with competition–colonization trade-offs. First, intermediate extents of disturbance (about 9–23% of landscape extent per year) to short-dispersing, competitively dominant seagrass can foster long-term spatial coexistence with broad-dispersing, competitively inferior burrowing shrimp via the spatial storage effect. Second, when holding the total extent of disturbance constant, the individual size and annual frequency of disturbance can alter the overall spatial pattern of seagrass loss across the landscape and thereby mediate the dominance, evenness, and clustering of these spatial competitors. Numerous small disturbances favor seagrass by reducing the time required for recolonization, allowing it to quickly fill in gaps and exclude burrowing shrimp. Conversely, fewer large disturbances can cause time lags in seagrass recovery due to its comparatively limited dispersal, favoring rapid-colonizing burrowing shrimp by creating temporary refugia from competition. Third, irrespective of disturbance size or frequency, the dispersal ability of superior competitors (seagrass), the competitive ability of inferior competitors (burrowing shrimp), and the reproduction and survival of both competitors can be important to mediating coexistence.

Together, these findings indicate that disturbance size, frequency, and their interaction can mediate coexistence by altering the duration of time over which inferior competitors can escape competitive exclusion. Beyond the many coastal ecosystems home to seagrass and burrowing shrimp, our conclusions may apply broadly to heterogeneous landscapes containing competitive communities with clear interspecific differences in the response to disturbance, the strength of competitive exclusion, and the rate of colonization, especially when recovery depends on the spatial pattern of disturbance due to species dispersal attributes. Our results also suggest that management of disturbance size and frequency can maximize landscape-scale biodiversity or, alternatively, tip the balance of competition to favor the conservation of imperiled species (e.g., seagrass) or eradication of pests (e.g., burrowing shrimp) or non-native taxa.

Our findings demonstrate that intermediate extents of annual disturbance can maximize coexistence and evenness in our two-species competition–colonization trade-off system through the spatial storage effect (Chesson 2000, Roxburgh et al. 2004, Sears and Chesson 2007). This result supports the intermediate disturbance hypothesis (Connell 1978) and is consistent with earlier theoretical and empirical studies showing that patchy disturbance improves coexistence by reducing competition for limiting resources (summarized in Amarasekare 2003, Roxburgh et al. 2004, Sheil and Burslem 2013, Huston 2014). In our study, disturbance to seagrass did not simply delay eventual competitive exclusion, but instead yielded long-term stable coexistence (Appendices S2 and S5). Our results also align with non-spatial competition models showing that agents of density-independent mortality, such as disturbance, can strongly mediate coexistence (Holt 1985).

We found that coexistence was possible only within a fairly limited combination of disturbance sizes and frequencies in which burrowing shrimp were able to colonize disturbed patches and reproduce prior to being displaced by encroaching seagrass. The delicate balance of disturbance characteristics that we found necessary for coexistence is consistent with an earlier generic competition–colonization trade-off model which showed that long-term coexistence was only possible for a narrow range of intermediate disturbance frequencies (Roxburgh et al. 2004). Importantly, however, competitive communities in nature may not be characterized by equilibrium conditions and a much broader set of disturbance regimes may delay competitive exclusion long enough for other local and regional coexistence mechanisms to sustain biodiversity (Huston 1979, 2014).

Examinations of the intermediate disturbance hypothesis typically focus on variation in only one aspect of disturbance (Mackey and Currie 2001, Hughes et al. 2007), such as studies showing that intermediate disturbance extent increases boreal plant diversity (Mayor et al. 2012), intermediate disturbance frequency promotes the coexistence of sessile rocky intertidal flora and fauna (Sousa 1979), and intermediate disturbance intensity enhances the coexistence of desert plants (Guo 1996). Our study builds upon these earlier works by demonstrating that multiple disturbance attributes (size and frequency) can interact to structure biodiversity in competitive communities. Variation in the individual size and annual frequency of disturbance changed the spatial pattern of seagrass loss, thereby mediating the persistence of burrowing shrimp and the relative dominance of both species. Under similar total extents of disturbance, large infrequent disturbances tended to improve the

strength and stability of coexistence over smaller frequent ones. These results agree with and extend earlier theoretical work showing that increasing spatial correlation of disturbance can favor species with broad dispersal and disadvantage those with limited colonization ability (Moloney and Levin 1996, Banitz et al. 2008, Miller et al. 2012, Liao et al. 2016).

Across all disturbance regimes, burrowing shrimp showed greater spatial clustering than seagrass, probably because they were outcompeted at relatively low seagrass densities, forcing them to the core of disturbed areas, as observed in field studies (Castorani et al. 2014). The positive effect of spatially-autocorrelated disturbance for inferior competitors may be stronger for species in which settlement and recruitment are positively associated with the local density of adults (Banitz et al. 2008), such as organisms that respond positively to conspecific settlement cues (Woodin 1976). These findings for seagrass and burrowing shrimp may extend to other systems characterized by regular, repeated disturbance and clear interspecific competition–colonization trade-offs, especially when rates of recovery depend on the spatial pattern of disturbance, such as competition between vegetatively-spreading and wind-dispersed plants (Liao et al. 2016).

Sensitivity analysis indicated that, within the range of coexistence, abundances of competing species may be governed chiefly by the competitiveness of the fast-colonizing inferior competitor (burrowing shrimp), the colonization rate of the slow-colonizing superior competitor (seagrass), and the reproduction, survival, and carrying capacity of both species. Disturbance size and frequency had only modest effects on the relative importance of these and other biological parameters. Our finding that reproduction is important to the persistence of both species is consistent with generic competition–colonization trade-off models (e.g., Klausmeier 1998) and empirical metapopulation models (e.g., Castorani et al. 2017, Johnson et al. 2018) which show that variation in propagule production can be as important or more important than variation in successful long-distance dispersal.

Our results are consistent with earlier studies demonstrating that the rate of competitor recovery from disturbance can mediate coexistence (Huston 1979, 2014). Within the context of our study system, this finding supports the notion that processes that reduce seagrass clonal spread (e.g., light limitation; Ochieng et al. 2010) will enhance the persistence of burrowing shrimp. By contrast, variation in the strength of seagrass competitive exclusion had minimal importance to burrowing shrimp populations because even low densities of eelgrass rapidly exclude ghost shrimp (Brenchley

1982, Harrison 1987, Castorani et al. 2014). Likewise, processes that enhance the survival and reproduction of burrowing shrimp (e.g., reduced predation; Posey 1986b, Dumbauld et al. 2008) or increase sediment turnover and burial of seagrass seeds by burrowing shrimp (e.g., warming; Berkenbusch and Rowden 1999) should promote burrowing shrimp populations. Hence, understanding seagrass–burrowing shrimp interactions would be improved by resolving how ghost shrimp bioturbation affects seagrass seedling mortality (which has only been addressed in a single study; Dumbauld and Wyllie-Echeverria 2003). Our finding that variation in the lateral movement rate of burrowing shrimp was unimportant to their populations supports the idea that over broad scales, larval recruitment has an overwhelming influence on the colonization of disturbances to seagrass, whereas post-settlement movement is probably more important over smaller scales in space and time (Castorani et al. 2014, Dumbauld and Bosley 2018). Our results suggest that seagrass persistence is insensitive to variation in burrowing shrimp parameters and depends only upon changes in survival and reproduction (chiefly clonal propagation, but also seed production and recruitment). More generally, our finding that variation in species traits is vital to structuring coexistence and biodiversity reinforces conclusions drawn from competitive communities of annual plants (Turnbull et al. 2004), ants (Stanton et al. 2002), birds (Rodríguez et al. 2007), parasitic trematodes (Mordecai et al. 2016), and sessile invertebrates (Edwards and Stachowicz 2010).

Results from this and earlier studies (Banitz et al. 2008, Liao et al. 2016) indicate that altering the size and frequency of disturbance can be a useful tool for landscape-scale management of biodiversity and natural resources. In general, reducing the size of disturbance may support the persistence of slow-colonizing competitive dominants, such as many habitat-forming foundation species. Conversely, prescribing the total extent, individual size, and frequency of disturbance may aid in the eradication of undesired species, such as agricultural pests or non-native taxa, depending on their relative competitive rank and colonization ability. However, we stress caution in managing disturbances because competitive coexistence can be structured by interspecific differences in multiple traits (Seifan et al. 2013).

Within the context of our coastal benthic study system, our results suggest that reducing large disturbances to seagrass and promoting conditions that enhance reproduction (e.g., improved water quality) will maximize the persistence of seagrasses, which are imperiled globally (Waycott et al.

2009). In Washington State (USA), pesticides have been used for decades to eradicate burrowing shrimp from aquaculture sites because their bioturbation kills young oysters and reduces shellfish production (Feldman et al. 2000, Dumbauld et al. 2006). This practice has raised environmental concerns and recently caused conflict among oyster growers, managers, fishing communities, and the public (Baker 2016). Together with prior field studies (Harrison 1987, Swinbanks and Luternauer 1987, Castorani et al. 2014), the results of our model sensitivity analysis indicate that management actions that increase the rate of seagrass spread, such as seeding, transplantation, or restoration of water quality, may reduce local burrowing shrimp abundances. Likewise, conservation of benthic marine predators such as Dungeness crab, cutthroat trout, sculpin, flounder, leopard sharks, and grey whales may help lower burrowing shrimp populations by reducing adult survival, reproductive output, and density (Posey 1986b, Weitkamp et al. 1992, Feldman et al. 2000, Dumbauld et al. 2008, Dumbauld and Bosley 2018). Similarly, our findings suggest that conservation of the many fish species that prey upon ghost shrimp larvae, such as herring and salmon, may constrain ghost shrimp populations (Feldman et al. 2000). Feedbacks between seagrass expansion, enhanced fish abundance, lower burrowing shrimp abundance, improved sediment stability, and improved water quality may lead to synergy among goals in seagrass conservation, oyster aquaculture, and fisheries management.

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Table 1. Description of model parameters and values of mean and range used. Sources for parameter values are listed below table.

Description	Notation	Values			Units	Sources
		Estimate	Min.	Max.		
Seagrass parameters						
Equilibrium density of adult leaf shoots	k_S	1,000	700	3,845	shoots per m^2	1–7
Annual survival of adult leaf shoots	μ_S	0.507	0.450	0.730	unitless	8
Annual asexual production of new leaf shoots	α_S	0.956	0.551	1.455	unitless	8
Annual distance of lateral shoot spread	d	1.26	0	2.26	m per y	7, 9–11
Annual proportion of asexually-produced shoots spreading laterally	l	0.05	0.01	0.20	unitless	7
Equilibrium density of seeds	k_E	9,321	7,997	13,700	seeds per m^2	12–15
Annual seed production	σ	2.42	0	17	seeds per leaf shoot per y	3, 14, 16–18
Standard deviation of seed dispersal kernel	ω	3.19	3.10	3.27	m	19, 20
Seed recruitment	γ	0.0128	0	0.36	leaf shoots per seed per y	13, 14, 19, 21–23
Burrowing shrimp parameters						
Equilibrium density of adults	k_B	250	5	700	adults per m^2	7, 24–33
Annual survival of adults and juveniles	μ_B	0.62	0.24	0.79	unitless	32, 33
Annual production of juveniles*	$\alpha_{B,t}$	2.8 ± 2.0	0	4.9	unitless	32, 34, 35
Annual distance of adult lateral movement	ζ	6.0	1.63	13.0	m	7, 28, 36

Maturation rate	ρ	⅓	¼	½	per year	32
Species interactions						
Reduction in burrowing shrimp abundance due to competition with seagrass	φ	0.0668	0.0123	0.121	per seagrass leaf shoot per m^2 per y	7
Mortality of seagrass seedlings due to burrowing shrimp bioturbation	ψ	0.0046	0.0016	1	per adult burrowing shrimp per m^2 per y	37

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*Annual proportional production of juvenile burrowing shrimp is shown as mean ± standard deviation because recruitment varied stochastically among years. This parameter was drawn randomly from a truncated normal distribution (see *Methods*).

Figure legends

Figure 1. Seagrass populations experience disturbances that vary in their size and frequency, and this variation was approximated using spatial population models. (A) Aerial images of seagrass meadows in northern California, USA, show patterns consistent with fewer large disturbances (left) and many small disturbances (right). Inset photograph in panel A shows a dense burrowing shrimp colony. (B) Simulated landscapes mimicked such variation in disturbance to seagrass (relative densities of seagrass and burrowing shrimp are shown in shades of green and pink, respectively; white areas show recent disturbances to seagrass). Photo credit: M.C.N. Castorani.

Figure 2. Population models captured the essential processes governing the dynamics of seagrass and burrowing shrimp populations, as well as their interactions. See *Methods* and *Table 1* for descriptions of state variables and parameters. Note that not all parameters are shown.

Figure 3. Increasing the total annual extent of disturbance (i.e., the combined area of the landscape disturbed each year; *x*-axis) caused (A) gradual declines in seagrass populations and (B) increases in burrowing shrimp populations beyond a threshold, but this effect was mediated by the individual size of disturbances (warmer colors indicate larger disturbances; note log scale). Abundances represent normalized (i.e., rescaled to a maximum of one) landscape-scale adult population sizes at quasi-equilibria. The zone of long-term coexistence, in which abundances of both species are >1% of population maxima, is between the vertical dashed lines.

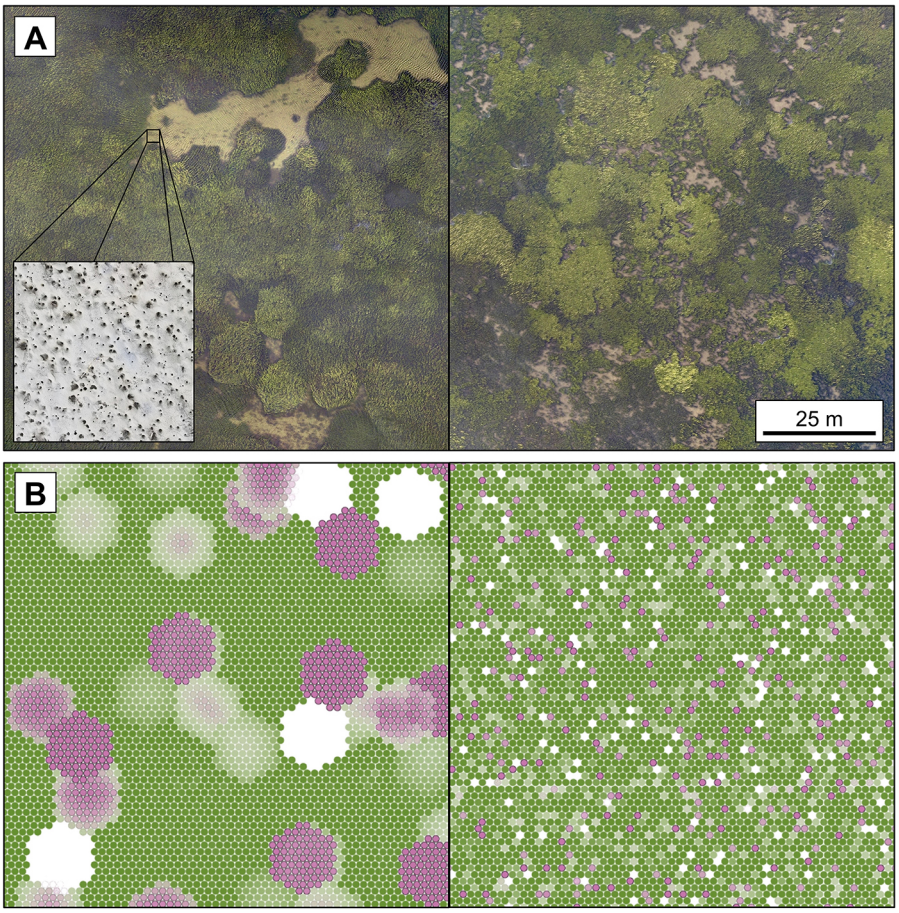
Figure 4. The size and frequency of disturbances interacted to alter (A) the total annual extent of disturbance across the landscape, (B) seagrass abundance, (C) burrowing shrimp abundance, and (D) species evenness (Simpson's *E*). Note that both axes are on a log scale. Abundances are normalized as in Fig. 3.

Figure 5. The individual size of disturbances mediated the negative effect of seagrass (*x*-axis; note log scale) on burrowing shrimp at the landscape scale. Hence for a given abundance of seagrass,

larger disturbances (warmer colors; note log scale) resulted in a greater abundance of burrowing shrimp. Abundances are normalized as in Fig. 3.

Figure 6. Larger, less frequent disturbances enhanced the spatial autocorrelation of (A) seagrass and (B) burrowing shrimp populations when compared to smaller, more frequent disturbances (larger values of Moran's *I* indicate greater spatial clustering). Burrowing shrimp were nearly always more clustered than seagrass because of strong competitive exclusion that forced burrowing shrimp to the interiors of areas experiencing seagrass loss (see Fig. 5 and Appendix S4: Fig. S1). Note that the color bar represents disturbance frequency on a log scale.

Figure 7. Results from the global sensitivity analysis showing the normalized relative importance of each biological parameter and its interactions with all other parameters in determining the abundance of seagrass (A; left panels) and burrowing shrimp (B; right panels) under four disturbance regimes that supported strong coexistence: a single very large disturbance (frequency = 1 per year, size = 21 m diameter); a few large disturbances (frequency = 13 per year, size = 7 m diameter); several medium disturbances (frequency = 102 per year, size = 3 m diameter); many small disturbances (frequency = 783 per year, size = 1 m diameter).



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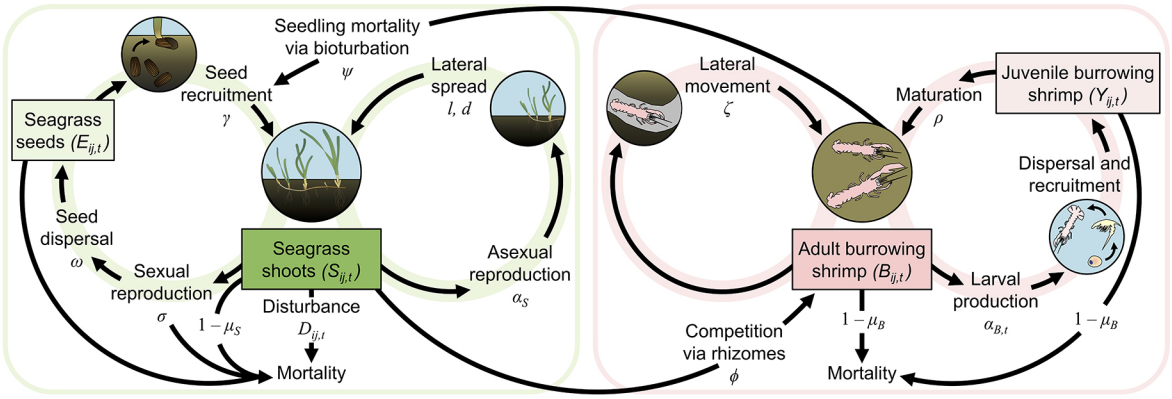

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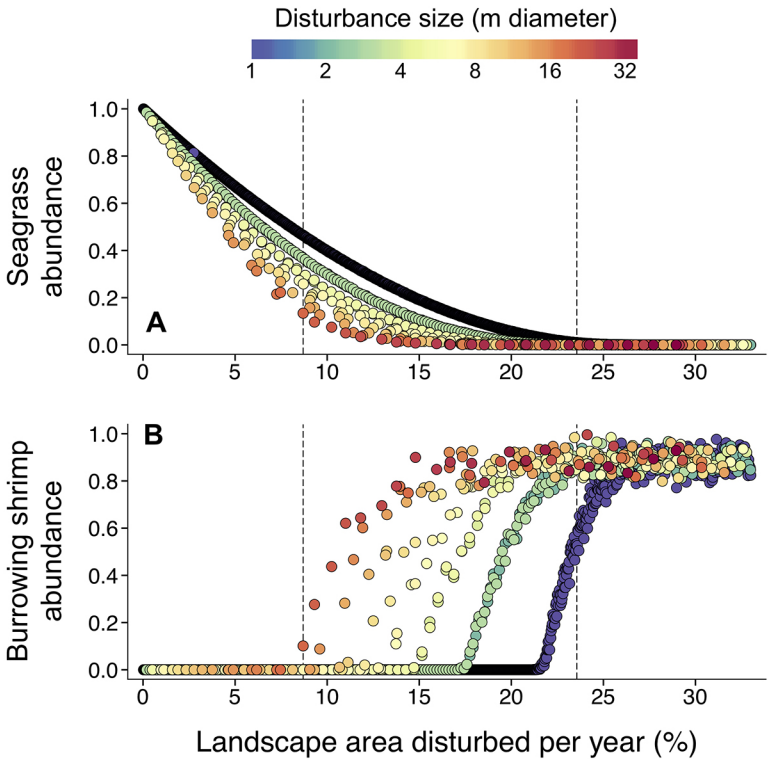

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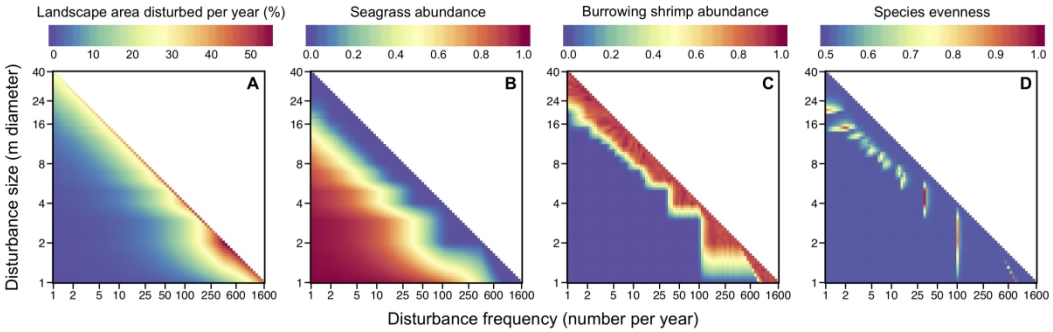

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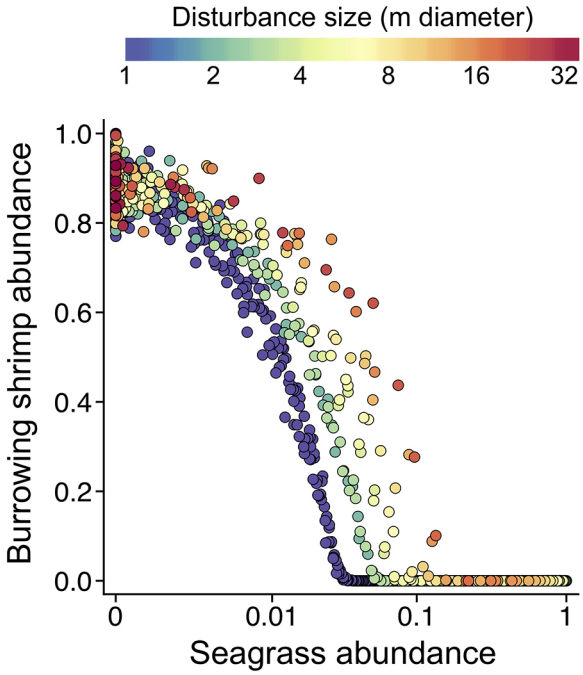

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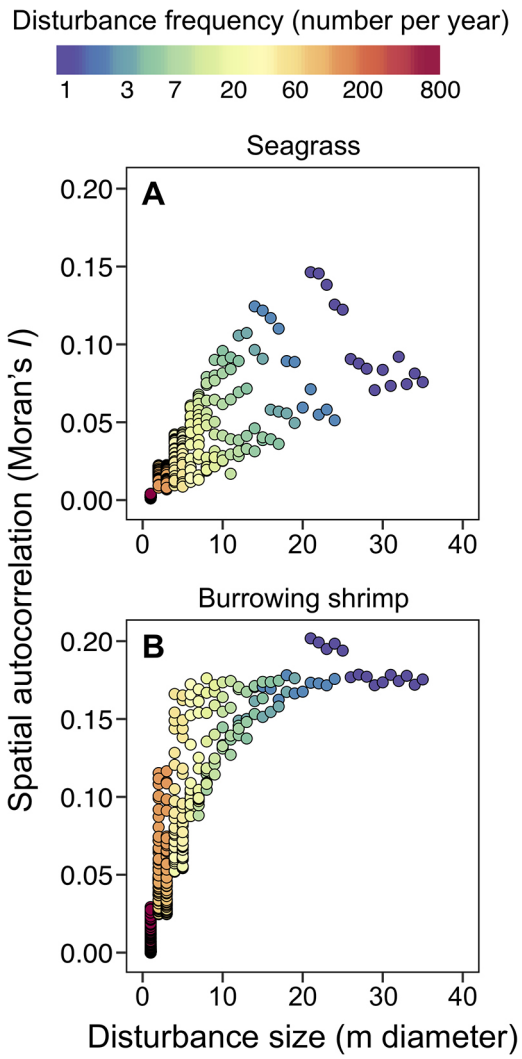

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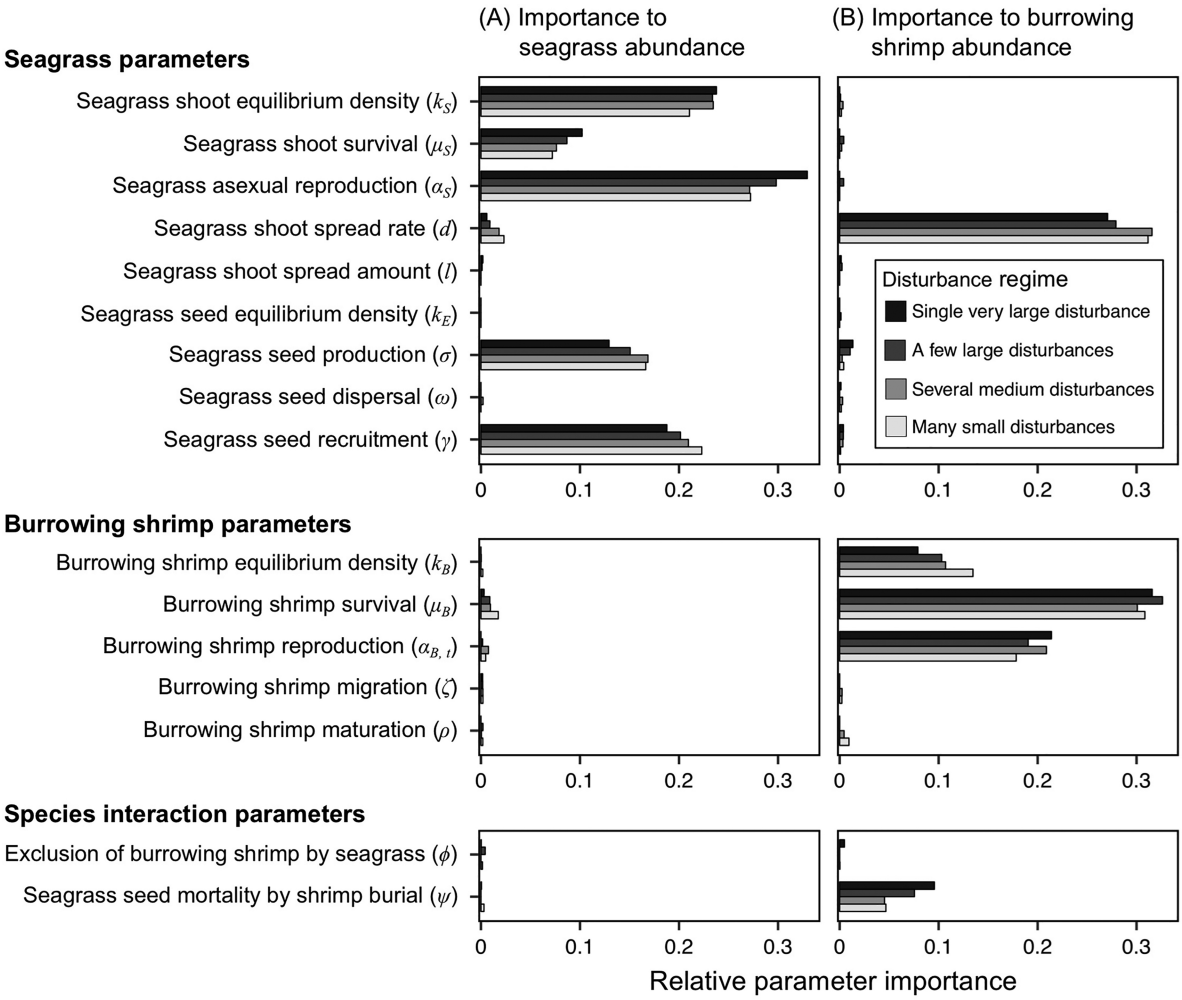

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